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GASEOUS EMISSIONS FROM PLANTS IN CONTROLLED ENVIRONMENTS

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2. ABSTRACT

Plant growth in a controlled ecological life support system may entail the build-up over extended time periods of phytotoxic concentrations of volatile organic compounds produced by the plants themselves. Ethylene is a prominent gaseous emission of plants, and is the focus of this report. The objective was to determine the rate of ethylene release by spring wheat, white potato, and lettuce during early, middle, and late growth stages, and during both the light and dark segments of the diurnal cycle. Plants grown hydroponically using the nutrient film technique were covered with plexiglass containers for 4 to 6 h. At intervals after enclosure, gas samples were withdrawn with a syringe and analyzed for ethylene with a gas chromatograph. Lettuce produced 10 to 100 times more ethylene than wheat or potato, with production rates ranging from 141 to 518 ng g-dry wt.$^{-1}$ h^{-1}. Wheat produced from 1.7 to 14.3 ng g-dry wt.$^{-1}$ h^{-1}, with senescent wheat producing the least amount and flowering wheat the most. Potatoes produced the least amount of ethylene, with values never exceeding 5 ng g-dry wt.$^{-1}$ h^{-1}. Lettuce and potatoes each produced ethylene at similar rates whether in the dark period or the light period. Ethylene sequestering of 33% to 43% by the plexiglass enclosures indicated that these production estimates may be low by one-third to one-half. These results suggest that concern for ethylene build-up in a contained atmosphere should be greatest when growing lettuce, and less when growing wheat or potato.

3. INTRODUCTION

Life support in the space environment places, among other problems, three related demands on a contained system; breathable air, drinkable water, and palatable food. All three requirements are linked to the life cycle of higher plants, which thus have become leading candidates to play major roles in a controlled ecological life support system, or CELSS (1,2).

Growing plants in contained systems is a relatively young science. Among the host of potential problems in a tightly closed system is the buildup of toxic compounds in the contained atmosphere. These compounds may come from a variety of sources, both animate and inanimate. Plants produce a wide array of organic compounds, and many if not all of these can eventually reach either the liquid or gaseous environment surrounding the plant. The primary concern of this project is the emission of gaseous compounds from plants.

3.1 PLANT GASEOUS EMISSIONS. Plants have been found to release measurable amounts of a variety of organic compounds, though often the amounts released are very small unless the plant is under some stress (3,4). Cuttings from red pine and paper birch seedlings produced acetaldehyde, ethanol, ethylene, and ethane after exposure to sulfur dioxide (4). Nance and Cunningham (5) found that excised wheat roots released acetaldehyde under both aerobic and anaerobic conditions, and Woodstock and Taylorson (6) noted that soybean seeds released ethanol and acetaldehyde when oxygen levels were reduced. Plants can also produce and release to the atmosphere an array of terpenes (7-10). Russian scientists found that excised leaf and root sections from radish, beets, tomatoes, potatoes, and carrots produced a variety of gases, including acetaldehyde, propionic aldehyde, acetone, ethanol, methanol, and propanol during enclosure for 24 h in an illuminated 100 ml glass container (11).

3.2 ETHYLENE AND PLANTS. Ethylene is a prominent gaseous emission of plants, and due to its effects on plant growth and development, it's considered a plant hormone (12,13). As a hormone it's unique in that it is a gas, and it can influence the same cells that produce it (12). Under normal conditions, gaseous ethylene is quickly dispersed and diluted in the atmosphere, requiring no special mechanism on the part of the plant to dispose of it after it has served its growth regulating function. However, in a closed system, ethylene concentrations can increase and induce a variety of plant responses. Due to its importance as a plant growth substance, its ubiquitous production by higher plants, and the ease of measurement, ethylene emissions were the focus of this project.

3.2.1 Effects of Ethylene on Plant Growth and Development. Practically every aspect of plant growth and development can be influenced by ethylene (12). The effects of ethylene may vary depending on the species, its developmental stage, and the ethylene concentration. Ethylene can promote seed germination, increase sprouting, inhibit cell elongation, cause

horizontal growth and swelling, prevent leaf expansion, reduce root elongation, stimulate root hair formation and root coiling, and increase or decrease flowering (12). Morison and Gifford (14) found that exposure to ethylene concentrations as low as 60 ppb for 36 days decreased leaf area and total dry weight of tomato and rice, and decreased height of rice.

One intriguing aspect of ethylene's effects on plants is its ability to induce subsequent ethylene production (15). Investigators found that a pulse of exogenously applied ethylene stimulated an increased endogenous ethylene production that influenced subsequent plant growth and development in orchids, carnations and sweet potato (16-18).

Ethylene is also released in response to stress imposed on a plant (3). So-called "stress ethylene" may be an adaptive plant response to a change in its environment, as the ethylene thus produced can stimulate accelerated senescence, abscission, wound healing, and increased disease resistance (13).

Ethylene may be essential for normal plant development. A tomato mutant presumably lacking the ability to produce any ethylene, grows abnormally unless ethylene, in concentrations as low as 5 ppb, is added to its environment (19).

3.2.2 Production Rates. Vegetative tissues can produce ethylene at rates from 0.05 to 1.25 ng g-fresh weight^{-1} h^{-1}, while fruits may produce from 0.01 to 19 ng g-fresh weight^{-1} h^{-1} (12,20). The rate of ethylene production varies with the species and the stage of plant development (12). Although there are many reports of ethylene production rates for different plant tissues, few studies have examined the basal ethylene emission rate for intact plants (21). Dhawan et al. (22) reported that several different intact sunflower shoots produced from 6 to 60 ng ethylene g-dry weight^{-1} h^{-1}.

3.2.3 Environmental Influences on Production Rates. As stated earlier, a variety of stresses will cause enhanced ethylene release by plants, and the relationship between some of these stresses and the ethylene response is often more reliable an indicator of plant stress than visible symptoms (3). But environmental factors need not reach stressful extremes before they can influence the production of ethylene by plants. Increased carbon dioxide levels caused a corresponding increase in ethylene emissions by intact sunflower shoots, and decreased carbon dioxide levels caused decreased ethylene levels (22). In both cases, the ethylene response was apparent within 15 min of the change in carbon dioxide concentrations. Horton (23) also noted that ethylene emission rates fell when carbon dioxide decreased.

Related to the carbon dioxide effect is the generally inhibitory effect of light on ethylene release (23). Kapuya and Hall (24), however, found different relationships between light and ethylene release depending on the species and the photoperiod. Kalanchoe daigremontana released more ethylene towards the end of the light period, Vicia faba ethylene release peaked at the onset of the light period, and ethylene release by Caltha polypetala

peaked at the start of the dark period and again shortly after onset of the light period (24).

Although depressed oxygen levels in air will stimulate ethylene production in barley and maize, the relationship between oxygen levels and ethylene release is often confounded with the physical effects of submersion (25). Ethylene is produced in all parts of a plant, thus when some part of a plant is submerged, ethylene will not be able to diffuse out of the submerged tissue as fast as out of tissue in air. The build-up of ethylene concentrations in submerged tissues will cause subsequent ethylene responses in those and other tissues (25).

Low temperatures reduced ethylene release by excised snap bean leaf disks (26). Ethylene release by apple and bean leaves changed by 30% in response to 5 C changes in air temperature from 20 C. As temperature increased, ethylene production increased, as temperature decreased, ethylene production decreased (27).

Clinostat experiments, where plants are continuously rotated to negate the effects of Earth's gravitational field, caused increased ethylene evolution and subsequent leaf epinasty (28,29).

3.3 OBJECTIVES. The objectives of this project were to examine the ethylene emission rates for wheat, potato, and lettuce at early, middle, and late growth stages, and during both the light and dark periods of the diurnal cycle.

4. MATERIALS AND METHODS

4.1 GAS MEASUREMENT. Measurement of trace gases was accomplished with gas chromatography using a Hewlett Packard 5880A Series Gas Chromatograph with a flame ionization detector (FID). A 25 cm stainless steel column, 2 mm outside diameter, filled with 80/100 mesh alumina was used for ethylene determinations. The oven was held at 30 C, the detector at 125 C. The nitrogen carrier gas flowed at 20 ml min^{-1}, hydrogen at 30 ml min^{-1}, and oxygen at 100 ml min^{-1}. Ethylene peaks were identified and quantified by comparison with standard gases at 100.1 and 8.1 ppm (Scott Specialty Gases, +2%), and dilutions of these standards to 0.10, 0.08, 0.05, and 0.04 ppm. Samples were taken with a 1 ml gas-tight syringe.

4.2 PLANT GROWTH. Plants were grown in the Plant Laboratory at the Life Science Support Facility, Hangar L, Kennedy Space Center (KSC), in a hydroponic system based on the nutrient film technique (NFT) (30). The system consisted of pie-shaped, 5 cm deep, PVC trays with a surface area of 0.175 m^2. A nutrient solution was pumped into the wide end of a tray at the rate of 1 L min^{-1}, flowed along the bottom reaching a depth of 0.5 to 1.0 cm, and allowed to drain out at the narrow end of the tray.

The nutrient solution consisted of a half-strength Hoagland's solution (Table 1) maintained at pH 6.0 automatically with a pH controller (Cole Parmer Model 5997-30) dispensing a 1.25% v/v solution of HNO_3. The 30 L nutrient solution reservoir was changed weekly.

Trays were placed on a bench or in an Environmental Growth Chamber, Model M13, in the Plant Laboratory. All plants were grown under high pressure sodium lamps with a 14/10 h day/night cycle. Photosynthetic photon flux density averaged 685 umol m^{-2} s^{-1} in the growth chamber, and 230 umol m^{-2} s^{-1} on the bench. Temperatures were maintained at 23 C in the growth chamber and 27 C on the bench. Relative humidity averaged 61% in the growth chamber and 49% on the bench.

Lettuce and potatoes in the growth chamber were kept on separate nutrient delivery systems, two trays per 30 L reservoir. The two trays of wheat and two trays of potato on the bench all shared a single 30 L reservoir and nutrient delivery system.

4.2.1 Wheat. Spring wheat seeds, cv. Yecora Rojo, were soaked for 15 min in deionized, filtered-sterilized water to remove the fungicide. The seeds were rinsed three times with the sterilized water, then wrapped in sterile paper towels and placed in a sterile plastic bag. The bagged seeds were refrigerated at 6 C for 4 days. At planting, approximately 450 seeds were placed between double strips of polyethylene film suspended at the surface of the nutrient solution in each of two PVC trays. During germination the tray was covered with a clear plexiglass hood. Four days after planting the hood was removed and a grid of plastic-coated wire mesh (6 cm by 5 cm) was placed 20 cm above the tray to provide support for the wheat stalks as they elongated. Two trays were placed on the bench and two were placed in the growth chamber.

4.2.2 Potato. Four potato plantlets, cv. Denali, in continuous in vitro culture in 15 cm by 2 cm test tubes on a modified MS agar medium with 3% sucrose (31), were removed 35 days after in vitro propagation and suspended at the surface of the nutrient solution in two PVC trays, two plantlets per tray. These two trays were placed on the bench in the Plant Laboratory. Stainless steel rods were attached to the each tray one month later for support of the top-heavy shoots. Two trays, each started with three plantlets each of two cultivars, Denali and Norton, were placed in the growth chamber.

4.2.3 Lettuce. Lettuce seeds, cv. Waldman's Green, were placed between double strips of polyethylene film suspended at the surface of the nutrient solution in two PVC trays placed in the growth chamber.

4.3 EXPERIMENTAL DESIGN

At early, middle, and late growth stages, plexiglass covers were fitted around the trays to provide an airtight seal for a period of 4 to 6 h during either the light or the dark period. Only flourescent lights were on during

the light-period enclosure. All nutrient flow was stopped during enclosure, and a 1 cm deep pool of nutrient solution was left at the bottom of each tray. At intervals during enclosure, 1 ml gas samples were withdrawn through a septum port for ethylene analysis.

4.3.1 Wheat. Two trays of four-day old wheat seedlings in the growth chamber were enclosed (13.94 L volume) from 0900 to 1300 (all times are EDT). Gas samples were withdrawn 2 and 4 h after enclosure. A partial harvest was conducted after the 4-day test to calculate dry weight biomass estimates. Two trays of 43-day old wheat plants, in the process of flowering and located on the bench in the Plant Laboratory, were enclosed (65.73 L volume) from 0900 to 1500. Gas samples were withdrawn 4.5, 5, and 6 h after enclosure. A partial harvest was conducted after the 43-day test to calculate biomass estimates. The same two trays were enclosed (121.63 L volume) at 76 days, when seed set was complete, from 0900 to 1500. Gas samples were withdrawn 2, 4, and 6 h after enclosure. All shoots and roots were harvested after this test, dried at 70 C for 24 h, and weighed.

4.3.2 Potato. Two trays of twenty-day old potatoes in the growth chamber, containing three plants each of cultivars Denali and Norland on each tray, were enclosed (65.73 L volume) from 0900 to 1500. Gas samples were withdrawn 2, 4, and 6 h after enclosure. Shoots and roots were harvested after the test, dried at 70 C for 48 h, and weighed. Two trays on the bench in the Plant Laboratory, each holding two 65 day-old 'Denali' potato plants in the process of flowering, were enclosed (121.63 L volume) from 2200 to 0400. Gas samples were withdrawn 6 h after enclosure. The same two trays were enclosed (121.63 L volume) at 67 days from 0900 to 1500. Gas samples were withdrawn 2, 4, and 6 h after enclosure. After the 67-day test, all shoots and roots were harvested, dried at 70 C for 48 h, and weighed. The biomass estimates obtained from this harvest were used for both the 65 and 67-day potato tests to calculate ethylene production rates.

4.3.3 Lettuce. Two trays in the growth chamber were enclosed (13.94 L volume) from 0900 to 1500 at 9 and 15 days after seed placement. Gas samples were withdrawn 3 and 6 h after enclosure. The same two trays were enclosed (13.94 L volume) at 11 days from 2200 to 0400. Gas samples were withdrawn 6 h after enclosure. A partial harvest was conducted after the 9-day test, and used for calculating the dry weight biomass estimates for the 9 and 11-day tests. All shoots and roots in each tray were harvested after the 15-day test, dried at 70 C for 24 h, and weighed.

4.3.4 Blank Tray Tests. Empty PVC trays were closed with the plexiglass covers and monitored for ethylene production over a 6-h period under flourescent lights. Sixty ml of 100.1 ppm ethylene was injected into empty PVC trays with different size plexiglass covers attached (total volumes 13.94 and 65.73 L) in order to determine the amount of ethylene absorbed by the containers during a 6-h period. These enclosures were also under flourescent lights. One ml gas samples were withdrawn 15 min, 30 min, and 6 h after ethylene injection. Percent of ethylene remaining in the enclosure at each time was calculated.

5. RESULTS AND DISCUSSION

5.1 ETHYLENE EMISSIONS.

All three species tested produced measurable amounts of ethylene, ranging from over 350 ng g-dry wt.$^{-1}$ h^{-1} in seedling lettuce to less than 2 ng g-dry wt.$^{-1}$ h^{-1} in senescing spring wheat (Table 5). Lettuce produced one to two orders of magnitude more ethylene than either wheat or potato (Table 5). Potato produced the least ethylene of the three species tested, with the exception of senescing wheat (Table 5).

5.1.1. Wheat. Spring wheat, cv. Yecora Rojo, produced more ethylene during early vegetative growth and flowering than during the later stages of senescence (Table 2). Ethylene production was greatest during the flowering period, averaging 14.3 ng g-dry wt.$^{-1}$ h^{-1} in 43-day-old plants. By comparison, 76-day-old, senescing plants produced only 1.7 ng ethylene g-dry wt.$^{-1}$ h^{-1}.

5.1.2. White potato. Potato produced an average of 3 ng g-dry wt.$^{-1}$ h^{-1} over the entire 6-h enclosure period (Table 5). Although cultivars Denali and Norland both contributed to the production estimate for 20-day-old plants, 'Norland' provided most of the biomass. Thus the observation that plant age did not make a significant difference in ethylene production by potatoes is confounded by the cultivar differences at the two ages tested (Table 3).

5.1.3. Lettuce. Lettuce, cv. Waldman's Green, produced more ethylene at 9 days old than at 15 days old (Table 4), though at both ages lettuce produced well over 100 ng g-dry wt.$^{-1}$ h^{-1}. The greater production in the 9-day-old plants may have been due to the 42% of seedlings in the process of dying, which plants accounted for 30% of the total dry weight. At 15 days old, the healthy plants, averaging 34 per tray, were much larger and accounted for over 90% of the total dry weight.

5.1.4. Light Versus Dark Emissions. Although lettuce averaged more ethylene production during the dark period than during the light, the degree of variability associated with both measurements makes it impossible to draw conclusions (Table 6). Likewise, although potatoes produced slightly less ethylene during the dark period than during the light, the difference is too small to draw conclusions.

5.3 PLEXIGLASS, PVC, AND ETHYLENE.

Joined plexiglass covers and PVC trays did not produce measurable amounts of ethylene, either under flourescent or high pressure sodium lamps during 6-h tests. A 5 ppb lower limit of detection for ethylene means that less than 87 ng of ethylene was produced in the 13.94 L container and less than 412 ng was produced in the 65.73 L container.

The plexiglass/PVC containers did, however, sequester significant amounts of ethylene during 6-h periods under moderate flourescent lighting (Table 7). Although 84% of the injected ethylene remained in the contained 13 L atmosphere 15 min after injection, 6 h after injection only 67% was recoverable in the gas phase (Table 7). However, in the 65 L enclosure, ethylene disappearance after 6 h was not significantly greater than after just 15 min (Table 7). Percent recovery of injected ethylene was less in the 65 L enclosure than in the 13 L enclosure (Table 7).

As a result of the significant ethylene sequestering by the plexiglass/PVC enclosures, the ethylene emission rates reported here are probably low. As much as 37% of the ethylene produced by test plants in the 13 L enclosures, and up to 43% of that produced in the 65 L enclosures, may have been absorbed, adsorbed, or otherwise removed from the gas phase prior to sampling.

6. SUMMARY AND CONCLUSIONS

Hydroponic culture of lettuce in a closed atmosphere may produce significant amounts of ethylene, greater than that produced by either spring wheat or white potato. White potato, during vegetative or reproductive growth, produced less ethylene than either seedling lettuce or seedling or flowering wheat. Senescing wheat produced the smallest amount of ethylene measured.

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TABLE 1. The concentration of elements in the nutrient solution.

ELEMENT	CONCENTRATION
	millimoles L^{-1}
N	7.00
P	.50
K	3.00
Ca	2.50
Mg	1.00
S	1.00
	micromoles L^{-1}
Fe	50.00
Mn	3.70
Zn	.32
Cu	.13
Mo	.04
B	19.00

TABLE 2. The rate of ethylene emissions from spring wheat, cv. Yecora Rojo, at different ages grown hydroponically using the nutrient film technique.

AGE	STAGE OF DEVELOPMENT	NO. OF TRAYS	TRAY VOLUME (L)	ENCLOSURE TIME (EDT)	NO. OF HOURS	EMISSION RATE (ng/g-dry wt./h)	S.D.
4 days	seedling	2	13.94	0900-1300	4.0	10.7	1.6
43 days	flowering	2	65.73	0830-1300	4.5	13.4	4.4
				1300-1330	.5	12.2	4.4
				1330-1430	1.0	19.4	7.5
76 days	senescence	2	121.63	0900-1100	2.0	nd*	-
				1100-1300	2.0	3.3	2.7
				1300-1500	2.0	1.9	2.8

*not detectable

TABLE 3. The rate of ethylene emissions from white potato, cvs.* Denali and Norland, at different ages grown hydroponically using the nutrient film technique.

AGE	STAGE OF DEVELOPMENT	NO. OF TRAYS	TRAY VOLUME (L)	ENCLOSURE TIME (EDT)	NO. OF HOURS	EMISSION RATE (ng/g-dry wt./h)	S.D.
20 days	vegetative	2	65.73	0900-1100	2.0	6.7	.1
				1100-1300	2.0	1.6	.3
				1300-1500	2.0	1.9	.2
67 days	flowering	2	121.63	0900-1100	2.0	nd#	-
				1100-1300	2.0	3.2	4.4
				1300-1500	2.0	5.5	7.3

*Twenty-day-old plants were one-half 'Denali' and one-half 'Norland'. Sixty-seven-day-old plants were all 'Denali'.

#not detectable

TABLE 4. The rate of ethylene emissions from lettuce, cv Waldman's Green, at different ages grown hydroponically using the nutrient film technique.

AGE	STAGE OF DEVELOPMENT	NO. OF TRAYS	TRAY VOLUME (L)	ENCLOSURE TIME (EDT)	NO. OF HOURS	EMISSION RATE (ng/g-dry wt./h)	S.D.
9 days	seedling	2	13.94	0900-1200	3.0	518	444
				1200-1500	3.0	191	131
15 days	vegetative	2	13.94	0900-1200	3.0	219	48
				1200-1500	3.0	141	1

TABLE 5. Comparison of ethylene emissions from spring wheat, white potato, and lettuce grown hydroponically using the nutrient film technique.

SPECIES AND AGE	STAGE OF DEVELOPMENT	NO. OF TRAYS	TRAY VOLUME (L)	ENCLOSURE TIME (EDT)	NO. OF HOURS	EMISSION RATE (ng/g-dry wt./h)	S.D.
WHEAT:							
4 days	seedling	2	13.94	0900-1300	4.0	10.7	1.6
43 days	flowering	2	65.73	0830-1430	6.0	14.3	4.9
76 days	senescence	2	121.63	0900-1500	6.0	1.7	1.8
POTATO:							
20 days	vegetative	2	65.73	0900-1500	6.0	3.5	.2
67 days	flowering	2	121.63	0900-1500	6.0	2.9	1.0
LETTUCE:							
9 days	seedling	2	13.94	0900-1500	6.0	354.5	287.8
15 days	vegetative	2	13.94	0900-1500	6.0	179.6	23.4

TABLE 6. Comparison of light-period and dark-period ethylene emissions from lettuce and white potato grown hydroponically using the nutrient film technique.

SPECIES: ENCLOSURE TIME (EDT)	DIURNAL PERIOD	NO. OF HOURS	STAGE OF DEVELOPMENT	NO. OF TRAYS	TRAY VOLUME (L)	EMISSION RATE (ng/gdw/h)	S.D.
LETTUCE:							
0900-1500	light	6	seedling	2	13.94	354.5	287.8
2200-0400	dark	6	seedling	2	13.94	510.5	118.1
POTATO:							
0900-1500	light	6	flowering	2	121.63	2.9	1.0
2200-0400	dark	6	flowering	2	121.63	1.0	1.1

TABLE 7. Ethylene disappearance in different size plexiglass and PVC enclosures under flourescent lighting.

ENCLOSURE VOLUME (L)	NO. OF TRAYS	ETHYLENE INJECTED (ng)	TIME AFTER INJECTION (h)	ETHYLENE RECOVERED (ng)	S.D.	PERCENT RECOVERY (%)
13.94	2	7517	.25	6286	817	84
			.50	6058	124	81
			6.00	5068	260	67
65.73	2	7517	.25	4510	788	60
			.50	3663	407	49
			6.00	4280	582	57